METABOLISM AND NUTRITION

The Relationship of Body Composition, Feed Intake, and Metabolic Hormones for Broiler Breeder Females

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ABSTRACT Three hundred twenty Cobb 500 broiler breeder pullets at 21 wk of age were selected from a flock fed according to Cobb Breeder Management Guide specifications. One hundred sixty pullets at 21 wk of age were switched to ad libitum feeding, and the remaining 160 pullets continued to be control-fed. The pullets were photostimulated at 22 wk and maintained until 36.5 wk. Plasma samples were obtained, BW was determined, and hens were killed for determination of body composition at the following periods: 24 h prior to photostimulation, 2.5 wk after photostimulation, 24 h after first egg, and 36.5 wk following peak egg production. Compared with ad libitum-fed breeders, the restricted breeders had a higher percentage carcass protein and lower percentage carcass fat at all sampling periods. Total egg numbers were greater, and abnormal eggs were less for the restricted pullets compared with the ad libitum-fed pullets at 36.5 wk. Carcass percentage fat of ad libitum-fed pullets was positively related to plasma glucagon, insulin-like growth factor-II (IGF-II), and 17β -estradiol but negatively

related to plasma insulin, insulin/glucagon M ratio, insulin-like growth factor-I (IGF-I), thyroxine (T_4) , and triiodothyronine (T₃). Carcass percentage fat of feed-restricted pullets was negatively related to IGF-I, IGF-II, and T₄. The T₄ was the most important hormone for predicting the percentage carcass fat in ad libitum-fed pullets, and IGF-I was the most important hormone for predicting the percentage carcass fat in feed-restricted pullets. The percentage carcass protein for ad libitum-fed breeders was positively correlated to IGF-I, T₄, T₃, insulin/glucagon M ratio, and insulin. Carcass percentage protein for feed-restricted breeders was positively correlated to IGF-I, IGF-II, T₄, and glucagon. Stepwise regressions for predicting percentage carcass protein for breeders fed by both systems shows that T₃ and IGF-I concentrations were the most important for ad libitum-fed breeders, whereas IGF-II and T₄ were best for feed-restricted breeders. The hormone status of breeders may be a key indicator to help predict the body composition and thus support management decisions for maintaining optimum production.

Key words: body composition, feed intake, metabolic hormone, broiler breeder

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INTRODUCTION

There have been many reports comparing ad libitum vs. restricted feeding of different type diets on various aspects of welfare, growth, body composition, and egg production in broiler breeders (Robbins et al., 1988; Lilburn and Myers-Miller, 1990; Joseph et al., 2000; Hocking et al., 2002). A key problem associated with the feeding and management of modern breeder strains is the early feed restriction required to control their BW. To successfully produce sexual maturity and cause breeder pullets to come into persistent production with photostimulation, breeder pullets need to reach a physiological threshold and have adequate fleshing with optimum levels of protein mass and fat tissue available. There is

evidence to suggest that a minimum amount of body fat may be required for sexual maturity in broiler breeder hens (Bornstein et al., 1984). The relationship of body composition of breeder pullets and plasma hormone levels may be a key indicator for determining the needed physiological threshold of pullets. In ducks, turkeys, and broiler breeders, a rapid weight gain at sexual maturity has been shown to decrease egg production and is associated with the ovulation of 2 or more ova on the same day (Hocking, 1990). Hocking (1993) showed that multiple ovulations in breeders cause the release of ova into their body cavity, resulting in no oviposition. The incidence of multiple ovulations can be decreased by controlling BW gain with feed restriction during the period before sexual maturity (Hocking et al., 1989).

Nutritional status and the subsequent responses of key plasma metabolic hormones [insulin, glucagon, and triiodothyronine (T₃)] are important factors that determine the level of hepatic lipogenesis in birds (Hillgartner et al., 1995). Fasting and feeding low dietary

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protein concentrations have been shown to increase plasma growth hormone (GH) concentrations and decrease plasma insulin-like growth factor-I (IGF-I; Lauterio and Scanes, 1987) in different strains of chickens. McGuinness and Cogburn (1990) found a strong positive correlation (0.97) between the proportional change in plasma IGF-I concentrations and relative growth rate. Decuypere and Kuhn (1984) reported that T₃ was suppressed during feed restriction in growing birds but returned to normal levels following realimentation. McMurtry et al. (1988) also observed feed restriction significantly suppressed circulating T₃ levels in broilers. In mammals, several studies have indicated that feed intake, and its associated effects on metabolic rate, may be the triggering mechanism for changes in reproductive function (Renaville et al., 1993). Fluctuations in plasma hormones and substrates may provide signals that link metabolic status to the activation of the reproductive system. The overall goals of the research are to provide a potential indicator of when a flock has reached a mature BW and physiological threshold needed to successfully produce sexual maturity and to determine the hormones associated with carcass composition changes to better coordinate feed management during production.

The present study was conducted to observe how hormones might relate to fat deposition and carcass traits as a means to evaluate reproductive status prior to sexual maturity and during egg production and to observe the hormone status of the breeders fed ad libitum to determine the relationship of hormones to feed intake. The hormone level of ad libitum-fed breeders may be a valuable tool in selecting breeding stock to change progeny's feed intake.

MATERIALS AND METHODS

Stock and Management

One thousand Cobb 500 breeder pullets were reared in floor pens and fed restricted amounts of feed using a combination of controlled daily feeding and skip-aday feeding to provide pullets of a standard BW according to the Cobb Breeder Management Guide (Cobb-Vantress, 2002) until 21 wk of age. Three hundred twenty breeder pullets of similar BW were selected from this group of 21-wk-old pullets to conduct the research. Breeder pullets with a mean BW of 1.90 kg \pm 0.18 were allotted to the feed restriction treatment, and breeder pullets with a mean BW of 1.91 kg \pm 0.13 were utilized for the ad libitum-fed treatment. The breeder pullets were separated into 4 groups of 40 pullets per treatment and were housed in individual cages. Four groups of 40 pullets each (160 pullets) were fed a restricted amount of breeder I diet (2,860 kcal of ME/kg; 16.0% CP) similar to levels recommended by the Cobb Breeder Management Guide (Cobb-Vantress, 2002) from 21 wk through the laying cycle (Table 1). Four groups of 40 pullets each (160 pullets) were fed the same breeder I diet ad libitum

Table 1. Feed allocation program for broiler breeders¹

Week of age	Feed allotment (g/bird per d)	Notes
21	113	
22	118	Light stimulation
23	127	0
24	132	
25	139	5% egg production, 397 kcal of ME
26	151	001
27	160	
28	165	60% egg production, peak feed, 472 kcal of ME
29	165	
30	165	Peak egg production
31	164	001
32	163	
33	162	
34	161	
35	160	
36	159	

¹Based on recommendations of the Cobb 500 Breeder Management Guide (2002).

starting at 21 wk of age through termination of the experiment at 36.5 wk of age. Within the 2 feeding schemes, feed-restricted breeders and breeders fed ad libitum were divided into 4 physiological time groups for data collection. Twenty-one breeder pullets from each feeding regimen were killed by CO₂ asphyxiation on the day prior to photostimulation at 22 wk; 21 breeder pullets from each feeding regimen were killed 2.5 wk after photostimulation; 40 of the breeder pullets from each feeding regimen were killed within 24 h after laying their first egg; and a final group of 40 breeders from each feeding regimen was killed at 36.5 wk of age. The control-fed breeder hens were fed a daily amount of feed according to the Cobb Breeder Management Guide regardless of BW. To evaluate the plasma hormone status and the correlation to daily feed intake, the grams of feed consumed per day per kilogram of metabolic body weight (MBW) were utilized for both ad libitum and feed-restricted breeders. The MBW was determined for each breeder by the equation MBW = kg of BW $^{0.75}$. Because the feed intake was controlled in the feed-restricted pullets, the main separation of hormones per MBW was the range of BW instead of differences in feed consumption. The breeders fed ad libitum were evaluated to show individual feed intake and hormone differences correlated to MBW.

Each pullet's BW, egg weights, and feed consumption were determined weekly through 36.5 wk of age or until the pullet was killed. Mortality and egg production were determined on a daily basis during the experiment. The data collected when breeders were killed were BW, abdominal fat pad weight, number and weight of ovarian follicles, and weight of ovaries without follicles. All breeder pullets and hens were killed and bled within 4 h of feeding in the morning. Animal use protocol No. 03008 for the experiment was approved by the University of Arkansas Institutional Animal Care and Use Committee.

Each breeder carcass was frozen at -20°C before autoclaving. The carcasses were placed in trays covered with foil and autoclaved at 120°C for 15 h in an AMSCO 3053 sterilizer (Steris Corporation, Mentor, OH). The carcasses were homogenized after autoclaving using a Waring 4 L blender (Waring products division, Dynamics Corporation of America, New Hartford, CT). Subsamples were collected after grinding and freeze-dried in a Genesis SQ 12 EL Freeze drier (The Virtis Company, Gardiner, NY). Carcass protein and fat were analyzed according to AOAC (1990) to correlate the body mass with hormone levels. The percentage carcass fat and protein were reported on a dry matter basis. Five milliliters of blood were collected using EDTA as anticoagulant from the wing vein from each breeder prior to being killed. The blood samples were centrifuged with TJ-6 centrifuge (Beckman Coulter Inc., Fullerton, CA) for 10 min at 3,000 rpm, and the plasma was separated and stored frozen at -20°C. The frozen plasma was analyzed for leptin, glucagon, insulin, T₃, thyroxine (T₄), IGF-I, insulin-like growth factor-II (**IGF-II**), and 17β -estradiol.

Hormone Assays

Specific radioimmunoassays were used to determine plasma hormone concentrations. All samples were analyzed within 1 assay to avoid interassay variations. Double antibody radioimmunoassays were used to determine plasma concentrations of IGF-I with an intraassay CV of 2.8% (McMurtry et al., 1994), chicken IGF-II with intraassay CV of 3.7% (McMurtry et al., 1998), insulin with intraassay CV of 2.2%, (McMurtry et al., 1983), and leptin with intraassay CV of 3.9% (Evock-Clover et al., 2002). The T₃ and T₄ were determined as previously described (McMurtry et al., 1988) and had CV of 2.5 and 2.8%, respectively. Plasma glucagon (Linco Research Inc., St. Charles, MO) and estradiol-17B (Diagnostics Products Corporation, Los Angeles, CA) were determined using commercial kits with an intraassay CV of 1.9 and 3.7%, respectively. For glucagon analysis, an aliquot of plasma was stored in the presence of 1,000 KIU of aprotinin.

Statistical Analysis

The experimental birds were housed in individual cages. The experimental design was completely randomized using individual pullets as the experimental unit. There were 2 feed levels and 4 periods of observations. All the data were subjected to ANOVA analysis of SAS (SAS Institute, Cary, NC). Differences between means were evaluated using Fisher's protected least significant difference procedure. The correlation coefficients between percentage carcass fat, percentage carcass protein, and feed consumption per day per metabolic BW (FCPDMBW) with blood hormones within each feed level were determined by the SAS Corr procedure. The equations using blood hormones to predict percentage carcass fat, percentage carcass protein, and

FCPDMBW within each feed level were determined by multiple regression analysis with SAS software. The stepwise technique was used for variable selection for the multiple regression equation of percentage carcass fat, percentage carcass protein, and FCPDMBW, respectively.

RESULTS

Body Composition

Body composition of restricted and ad libitum-fed breeders at prestimulation, poststimulation, first egg, and 36.5 wk are shown in Table 2. The results indicated that BW was increased with breeder age (an exception was a lack of BW change between the first egg and 36.5 wk for the feed-restricted breeders) in both feeding systems. The ad libitum-fed pullets gained 423, 685, 741, and 1,290 g more BW during prestimulation, poststimulation, first egg, and overall 36.5-wk period, respectively, compared with the feed-restricted breeders. Both absolute fat pad weight and fat pad percentage of BW were increased with breeder age for both feeding systems. The ad libitum-fed breeders had 58, 68, and 107 g more fat pad weight at poststimulation, first egg, and 36.5-wk period, respectively, and 1.3, 1.2, and 1.4% higher fat pad percentage of BW at poststimulation, first egg, and 36.5-wk period than restricted breeders. Carcass percentage fat increased with breeder age, whereas carcass percentage protein decreased with breeder age in both restricted and ad libitum-fed breeders. Compared with ad libitum-fed breeders, the restricted breeders had 9.8, 9, 8, and 7.4% more carcass protein at prestimulation, poststimulation, first egg, and 36.5-wk period and 4.4, 13.3, 14.3, and 7.9% less carcass fat at prestimulation, poststimulation, first egg, and 36.5-wk period, respectively.

Feed Intake

The FCPDMBW is shown in Table 2. The results indicated that ad libitum-fed breeders consumed 27.3, 33.3, 40.2, and 8.6 g more feed at prestimulation, poststimulation, first egg, and 36.5-wk period than feed-restricted breeders, respectively.

Egg Production

The average total egg production per hen and the percentage of abnormal eggs are shown in Table 2. The results showed the feed-restricted breeders produced 14.9 more eggs per breeder through 36.5 wk, and the percentage of abnormal eggs was 9.2% lower compared with the ad libitum-fed breeders.

Ovary Weight and Follicles

The ovary parameters at different physiological periods are shown in Table 3. The results showed that the

Table 2. Body composition and performance data¹

	0	timulation wk)		timulation wk)	First	egg		teau 5 wk)
Variable	Ad libitum	Restricted	Ad libitum	Restricted	Ad libitum	Restricted	Ad libitum	Restricted
BW (g) Fat pad (g) Fat pad (%) ² Total eggs Abnormal eggs (%) ³ FCPDMBW (g) ⁴ Carcass fat (%) ⁵ Carcass protein (%) ⁵	2,567 ± 138° 17.1 ± 4.7 ^f 0.7 ± 0.2 ^f — 91.3 ± 20.5 ^a 25.6 ± 3.7° 53.4 ± 5.2 ^b	$\begin{array}{c} 2,144 \pm 166^{\rm f} \\ 13.0 \pm 9.1^{\rm f} \\ 0.6 \pm 0.4^{\rm f} \\ \hline \\$	3,637 ± 281° 99.4 ± 39.1° 2.7 ± 0.9° — 87.6 ± 9.5° 43.0 ± 4.3° 43.7 ± 3.0°	2,952 ± 282 ^d 41.3 ± 9.3 ^e 1.4 ± 0.3 ^e — 54.3 ± 5.1 ^{de} 29.7 ± 4.3 ^d 52.7 ± 3.4 ^b	4,255 ± 328 ^b 139.2 ± 43.5 ^b 3.2 ± 0.8 ^b — 90.5 ± 27.0 ^a 46.3 ± 4.1 ^a 42.1 ± 2.8 ^{ef}	$ 3,513 \pm 207^{c} 71.0 \pm 17.8^{d} 2.0 \pm 0.5^{d} $ $ 50.3 \pm 1.9^{e} 32.0 \pm 4.1^{d} 50.1 \pm 2.6^{c} $	$4,809 \pm 378^{a}$ 212.2 ± 56.8^{a} 4.4 ± 1.1^{a} 42.1 ± 12.4^{b} 12.9 ± 2.9^{a} 67.2 ± 10.8^{b} 47.9 ± 6.3^{a} 40.3 ± 4.5^{f}	$3,519 \pm 229^{c}$ 105.1 ± 24.4^{c} 3.0 ± 0.7^{bc} 57 ± 12.9^{a} 3.7 ± 0.7^{b} 58.6 ± 2.6^{cd} 40 ± 4.4^{c} 47.7 ± 3.6^{d}

^{a-f}Means within rows for same parameter for breeders fed ad libitum and restricted with different superscripts were significantly different (*P* < 0.05).

pullets fed ad libitum had 31.55 and 13.53 g heavier ovary weight compared with the feed-restricted pullets at first egg and the 36.5-wk period, respectively. The ovary weights were heavier when the pullets laid their first egg and following peak egg production (36.5 wk) than for ovary weights from the pullets before and after light stimulation for both restricted and ad libitum-fed pullets. The number of small atretic ovarian follicles was 0.68 more in ad libitum-fed pullets compared with restricted pullets. The ovarian stroma weight at first egg was 7.35 g heavier in ad libitum-fed pullets than in restricted pullets. The total large yellow follicles (LYF) weight followed the same trend as the LYF number and showed that ad libitum-fed breeders had 24.57 g heavier total LYF weight than restricted breeders at first egg and numerically heavier total LYF than restricted breeders at the postlight stimulation and 36.5 wk period. The number of LYF and the total weight of LYF decreased by 5.55 and 19.69 g and by 3.55 and 11.08 g at the 36.5-wk period compared with first egg in ad libitum-fed and feed-restricted breeders, respectively. The number of LYF and the total weight of LYF were 2.84 and 45.76 g and 3.17 and 34.92 g more at the 36.5-wk period than at postlight stimulation for ad libitum and feed-restricted breeders, respectively.

Hormone Levels

The different feeding systems had significant effects on circulating levels of key metabolic hormones prior to the onset of egg production (Table 4). Circulating insulin and T₃ levels were 2.16 and 1.13 ng/mL higher, and glucagon levels were 626.18 pg/mL lower in the ad libitum-fed pullets compared with restricted pullets just prior to light stimulation at 22 wk. There was a significant decline in insulin levels after first egg for breeder hens fed by both feeding systems. The highest insulin levels appeared at postlight stimulation and first egg for restricted breeders and at postlight stimulation and prelight stimulation for ad libitum-fed breeders. Insulin levels for ad libitum-fed breeders were 2.16 and 1.49 ng/mL higher than restricted breeders during the pre- and postlight stimulation period. In contrast, the glucagon levels were 626 and 241 pg/mL higher in restricted breeders compared with ad libitum-fed breeders at prelight stimulation and the 36.5-wk period, but

Table 3. Ovarian parameters¹

		timulation wk)	Postlight s (24.5	timulation wk)	First egg		Plateau (36.5 wk)	
Variable	Ad libitum	Restricted	Ad libitum	Restricted	Ad libitum	Restricted	Ad libitum	Restricted
Ovary weight (g) Stroma weight (g) Postovulatory follicles Atretic ovarian follicles	0.69 ± 0.24 ^d —	0.49 ± 0.14 ^d —	6.7 ± 3.9 ^d —				73.87 ± 15.35^{b} 11.37 ± 3.84^{ab} —	60.34 ± 8.6° 10.67 ± 3.22°
Number of LYF ² Total LYF weight (g)	_ _ _	_ _ _	$\begin{array}{c} - \\ 4.25 \pm 2.66^{c} \\ 15.02 \pm 9.06^{c} \end{array}$	$ \begin{array}{c} $		8.47 ± 1.79^{b} 55.9 ± 12.3^{b}	$ 7.09 \pm 2.08^{b} 60.78 \pm 17.72^{b} $	$ \begin{array}{c} - \\ 4.92 \pm 1.4^{c} \\ 44.82 \pm 16.9^{b} \end{array} $

 $^{^{}a-d}$ Means within rows for same parameter for breeders fed ad libitum and restricted with different superscripts were significantly different (P < 0.05).

¹All values represent the mean ± SEM of 21 (pre- and postlight stimulation) or 40 (first egg and plateau) observations.

²Fat pad weight expressed as a percentage of BW.

³Includes soft shell or shell-less, multiple eggs, and multiple soft shell eggs.

⁴Feed consumption per day per metabolic BW.

⁵Percentages of carcass fat and protein are on a dry matter basis.

¹All values represent the mean ± SEM of 21 (pre- and postlight stimulation) or 40 (first egg and plateau) observations.

²Large vellow follicles.

Fable 4. Plasma hormone levels¹

	Prelight stimulation (22 wk)	imulation wk)	Postlight (24.5)	Postlight stimulation (24.5 wk)	First	First egg	Pla (36.5	Plateau (36.5 wk)
$Variable^2$	Ad libitum	Restricted	Ad libitum	Restricted	Ad libitum	Restricted	Ad libitum	Restricted
Insulin (ng/mL)	3.76 ± 0.46^{a}	1.6 ± 0.32^{f}	4.05 ± 0.79^{a}	2.56 ± 0.51 ^{cd}	3.01 ± 0.34^{b}	$2.86 \pm 0.62^{\rm bc}$	$2.4 \pm 0.41^{\text{de}}$	2.04 ± 0.26^{e}
Glucagon (pg/mL)	104.92 ± 14.6^{d}	731.1 ± 28.44^{a}	110.4 ± 36.23^{d}	167.09 ± 34.6^{d}	$276.82 \pm 10.43^{\circ}$	166.09 ± 51.48^{d}	$337.66 \pm 24.00^{\circ}$	579.10 ± 135.42^{b}
Intogl ²	24.08 ± 8.48^{a}	1.42 ± 0.38^{f}	20.50 ± 7.74^{b}	9.49 ± 2.31^{cd}	8.61 ± 5.56^{d}	$12.06 \pm 3.89^{\circ}$	$5.90 \pm 3.93^{\circ}$	2.81 ± 1.77^{f}
$T_3 (ng/mL)$	1.50 ± 0.58^{a}	0.37 ± 0.17^{d}	1.23 ± 0.63^{b}	1.21 ± 0.39^{b}	$0.67 \pm 0.33^{\circ}$	$0.59 \pm 0.33^{\circ}$	$0.59 \pm 0.26^{\circ}$	0.51 ± 0.29^{cd}
173-Estradiol (pg/mL)	164.26 ± 65.35^{b}	$77.53 \pm 34.48^{\circ}$	414.82 ± 205.97^{a}	359.32 ± 153.95^{a}	383.79 ± 170.05^{a}	351.13 ± 104.61^{a}	185.01 ± 90.56^{b}	234.85 ± 155.52^{b}
$T_4 (ng/mL)$	9.43 ± 3.2^{a}	8.68 ± 2.37^{a}	4.77 ± 1.99^{c}	6.24 ± 1.38^{b}	5.44 ± 1.6^{b}	5.59 ± 1.72^{b}	$5.77 \pm 1.86^{\text{b}}$	6.11 ± 2.01^{b}
Leptin (ng/mL)	13.28 ± 1.98^{a}	10.86 ± 1.56^{d}	12.93 ± 1.99^{ab}	11.50 ± 1.74^{cd}	12.31 ± 2.46^{abc}	10.85 ± 2.41^{d}	12.03 ± 3.73^{abcd}	$11.55 \pm 2.94^{\text{bcd}}$
IGF-I (ng/mL)	$15.3 \pm 6.33^{\text{de}}$	56.95 ± 22.1^{a}	$9.16 \pm 4.64^{ m ef}$	37.44 ± 8.12^{b}	7.19 ± 3.7^{f}	19.09 ± 9.37^{d}	8.76 ± 4.07^{ef}	26.09 ± 16.47^{c}
IGF-II (ng/mL)	58.64 ± 7.94^{d}	197.74 ± 45.3^{a}	71.45 ± 10.66^{d}	$87.85 \pm 14.27^{\circ}$	$90.44 \pm 7.89^{\circ}$	$88.92 \pm 12.59^{\circ}$	$98.64 \pm 16.12^{\circ}$	116.94 ± 35.75^{b}

 a^{-4} Means within rows for same parameter for breeders fed ad libitum and restricted with different superscripts were significantly different (P < 0.05)

All values represent the mean ± SEM of 21 (pre- and postlight stimulation) or 40 (first egg and plateau) observations. = insulin-like growth factor. 2 Intogl = M ratio of plasma insulin/glucagon; T_3 = triiodothyronine; T_4 = thyroxine; IGF

glucagon was 110.73 pg/mL lower than ad libitum-fed breeders at first egg. The changes for the insulin/glucagon M ratio (intogl) were similar to the trend in glucagon during different physiological periods. The intogl was 24.08 ± 8.48 vs. 1.42 ± 0.38 for the ad libitum-fed and feed-restricted pullets, respectively, prior to light stimulation. This ratio increased in the restricted group to 12.06 ± 3.89 as the pullets began to lay eggs, whereas it declined in the ad libitum-fed group to 8.61 ± 5.56 during this same time. As egg production progressed to 36.5 wk, both groups exhibited a decline in the intogl (Table 4). The T₃ levels were higher in ad libitum-fed breeders than in restricted breeders at the prelight stimulation period, but there were no significant differences thereafter for breeders from the 2 feeding systems. The T₄ level was 1.47 ng/mL higher in restricted pullets than in ad libitum-fed breeder pullets at postlight stimulation period. The T₄ levels were not significantly different for the 2 feeding systems at other physiological periods. The 17β -estradiol level was 87 pg/mL higher in ad libitum-fed breeders than in restricted breeders at the prelight stimulation period. There were no differences in 17β -estradiol between breeders from the 2 feeding systems for other periods. The leptin levels were 2.42, 1.43, and 1.46 ng/mL lower in feed-restricted pullets compared with the ad libitum-fed pullets at prelight stimulation, postlight stimulation, and first egg periods, respectively. There was no significant difference in the leptin level at the 36.5-wk period for the breeders fed by the 2 feeding systems. The plasma levels of IGF-I and IGF-II were 41.65, 139.1; 28.28, 16.4; 11.9, 1.52; and 17.33, 18.3 ng/mL higher in feed-restricted pullets compared with the ad libitum-fed pullets at prelight stimulation, postlight stimulation, first egg, and at the 36.5-wk period, respectively. There was a significant decline in IGF-I in the feed-restricted group at first egg compared with the feed-restricted pullets at the other periods. The ad libitum-fed breeders also had the lowest IGF-I level at first egg, but the level was not significantly lower than the IGF-I levels from the ad libitum-fed breeders at postlight stimulation and the 36.5-wk period.

Correlation Between Hormones, Feed Intake, and Carcass Composition

The correlation coefficients between the plasma hormone levels and feed intake for ad libitum-fed pullets are shown in Table 5. The results indicated that FCPDMBW was positively related with insulin (P=0.0205), intogl (P=0.0397), leptin (P=0.021), and T_3 (P=0.0446) but negatively related with IGF-II (P=0.0102). A stepwise regression for predicting FCPDMBW for ad libitum-fed pullets from hormone levels (Table 6) showed that an index consisting of IGF-I + IGF-II produced an R^2 of 0.087 (P=0.0567). The correlation coefficients between the plasma hormone levels and percentage carcass fat for ad libitum-fed pullets are shown in Table 5. The results indicated that percentage carcass fat of ad libitum-fed pullets was positively related with

Table 5. Correlation coefficients between FCPDMBW, percentage of carcass fat, and percentage of carcass protein with plasma hormones for ad libitum-fed breeders²

	Glucagon	Insulin	Intogl	IGF-I	IGF-II	Leptin	Estradiol	T_4	T ₃
FCPDMBW	-0.0504	0.2188	0.1947	0.0273	-0.2418	0.2178	0.1371	-0.0644	0.1902
	0.5979	0.0205	0.0397	0.7751	0.0102	0.021	0.1496	0.4999	0.0446
Carcass fat (%)	0.1909	-0.3291	-0.4463	-0.3243	0.2882	-0.0547	0.2201	-0.5281	-0.5216
	0.045	0.0004	< 0.0001	0.0005	0.0023	0.5706	0.0208	< 0.0001	< 0.0001
Carcass protein (%)	-0.1078	0.2935	0.3874	0.4253	-0.1742	0.0614	-0.1442	0.4499	0.4585
•	0.2644	0.0020	< 0.0001	< 0.0001	0.0714	0.5279	0.1364	< 0.0001	< 0.0001

¹Feed consumption per day per metabolic BW.

glucagon (P = 0.045), IGF-II (P = 0.0023), and 17β -estradiol (P = 0.0208) but negatively related with insulin (P =0.0004), intogl (P < 0.0001), IGF-I (P = 0.0005), T₄ (P < 0.0004) 0.0001), and T_3 (P < 0.0001). A stepwise regression for predicting percentage carcass fat for ad libitum-fed pullets using hormone levels (Table 6) indicated that an index consisting of T_4 + intogl + T_3 + IGF-I + IGF-II + 17β -estradiol provided an R² of 0.5843 (P = 0.0211). The percentage carcass protein of ad libitum-fed breeders was positively correlated to T_4 (P < 0.0001), T_3 (P <0.0001), IGF-I (P < 0.0001), intogl (P < 0.0001), and insulin (P = 0.002; Table 5). A negative correlation of IGF-II with percentage carcass protein for the ad libitum-fed breeders (-0.1742) was also close to being significant (P = 0.07). A stepwise regression for predicting the percentage carcass protein for ad libitum-fed breeders using hormone levels (Table 6) shows that an index consisting of T_3 + IGF-I + IGF-II + T_4 provided an R^2 of 0.505 (P = 0.0092).

The percentage carcass fat of feed-restricted breeders was negatively correlated to IGF-I (P < 0.0001), IGF-II (P = 0.0001), and T₄ (P = 0.0003; Table 7). The most important hormone for predicting percentage carcass fat in feed-restricted breeders was IGF-I ($R^2 = 0.1632$, <0.0001), however adding T₄ and glucagon levels during

stepwise regression analysis improved the correlation ($R^2 = 0.264$; P = 0.0118).

The percentage carcass protein of feed-restricted breeders was positively correlated to glucagon (P = 0.0014), IGF-I (P < 0.0001), IGF-II (P < 0.0001), and T₄ (P < 0.0001; Table 7). The percentage carcass protein of feed-restricted breeders was negatively correlated to insulin (P = 0.0002), intogl (P = 0.0075), and 17β -estradiol (P < 0.0001). A stepwise regression for predicting the percentage carcass protein of feed-restricted breeders showed that the index combination of IGF-II, T₄, glucagon, and insulin levels produced a correlation of $R^2 = 0.4448$ (P = 0.0187; Table 8). The addition of leptin to the index slightly increased the correlation ($R^2 = 0.4625$), however the index for predicting percentage carcass protein was nonsignificant (P = 0.0786).

DISCUSSION

Body Composition, Feed Consumption, and Egg Production

The study compared the effects of feed restriction vs. ad libitum feeding of broiler breeders on body composition, feed intake and plasma hormone levels during the

Table 6. Stepwise regression for predicting FCPDMBW, percentage of carcass fat, and percentage of carcass protein with plasma hormone levels for ad libitum-fed breeders

Step	Variable entered ²	\mathbb{R}^2	F-value	<i>P</i> > <i>F</i>
FCPDMBW	1 IGF-II	0.056	6.47	0.0124
	2 IGF-I	0.087	3.71	0.0567
	3 T ₄	0.106	2.20	0.1410
Carcass fat (%)	1 T ₄	0.2788	41.76	< 0.0001
, ,	2 Intogl	0.4346	29.47	< 0.0001
	3 T ₃	0.4851	10.41	0.0017
	4 IGF-I	0.5305	10.13	0.0019
	5 IGF-II	0.5622	7.53	0.0071
	6 Estradiol	0.5843	5.48	0.0211
	7 Glucagon	0.5961	2.99	0.087
Carcass protein (%)	1 T ₃	0.2131	28.43	< 0.0001
1 , ,	2 IGF-I	0.4035	33.19	< 0.0001
	3 IGF-II	0.4708	13.11	0.0005
	4 T ₄	0.5050	7.04	0.0092
	5 Intogl	0.5131	1.67	0.1989
	6 Estradiol	0.5183	1.09	0.2982

¹Feed consumption per day per metabolic BW.

²For each pair, top number is the correlation coefficient and bottom number is the *P*-value. IGF = insulin-like growth factor; T_4 = thyroxine; Intogl = M ratio of plasma insulin/glucagon; T_3 = triiodothyronine.

 $^{^{2}}$ IGF = insulin-like growth factor; T_{4} = thyroxine; Intogl = insulin/glucagon M ratio; T_{3} = triiodothyronine.

Table 7. Correlation coefficients between percentage of carcass fat and percentage of carcass protein with plasma hormones for feed-restricted breeders¹

	Glucagon	Insulin	Intogl	IGF-I	IGF-II	Leptin	Estradiol	T_4	T ₃
Carcass fat	-0.06769 0.4803	0.12189 0.2046	0.02187 0.8206	-0.40394 <0.0001	-0.36714 0.0001	-0.00524 0.9564	0.17705 0.0630	-0.33484 0.0003	-0.02137 0.8238
Carcass protein	0.2994 0.0014	-0.3488 0.0002	-0.2536 0.0075	0.4779 <0.0001	0.5677 <0.0001	0.0433 0.6518	-0.3876 <0.0001	0.4480 <0.0001	-0.0506 0.5974

 $^{^{1}}$ For each pair, top number is the correlation coefficient and bottom number is the P-value. Intogl = M ratio of plasma insulin/glucagon; IGF = insulin-like growth factor; T_{4} = thyroxine; T_{3} = triiodothyronine.

pullet-to-breeder transition period. It has been suggested that excessive BW gain, brought on by overfeeding of pullets during the reproductive development phase of production, accelerates ovarian follicular maturation such that more ovulations occur than the oviduct can effectively process (Siegel and Dunnington, 1985). This leads to an increase in the production of defective or nonsettable eggs. The higher incidence of abnormal (nonsettable) eggs produced by the ad libitum-fed group in this study supports that suggestion. The data in Table 2 shows that feed-restricted breeders had higher total egg production, fewer abnormal eggs, and consumed less feed than breeders fed ad libitum. The findings were in agreement with Hocking et al. (2002) who found that compared with ad libitum feeding, conventional feed restriction resulted in a proportional decrease in average daily feed consumption of 0.6 during rearing and a proportional decrease of 0.2 during early lay. Hocking et al. (2002) also found restricted pullets produced more eggs and more settable eggs with fewer abnormal eggs than breeders fed ad libitum. Renema et al. (1999a) found that BW, absolute abdominal fat pad weight, and the percent carcass lipids of ad libitum-fed pullets were greater than those of feed-restricted pullets at sexual maturity and the percentage of carcass protein, ash, and water of feed-restricted pullets were greater than those of ad libitum-fed pullets. The findings were in agreement with the results in Table 2 reported herein which shows the breeders with restricted feeding had lighter BW, less absolute abdominal fat pad weight, less carcass percentage fat and higher carcass percentage protein than breeders fed ad libitum.

The results of the total egg production and percentage of abnormal eggs shown in Table 2 indicated that the total egg production was higher and the percentage of abnormal eggs was lower for pullets that were feed restricted compared with the ad libitum-fed pullets. This was in agreement with Hocking et al. (1994) who reported that the peak rate of egg production was higher in restricted pullets than in ad libitum-fed pullets and the difference was maintained to the end of the experiment. Robbins et al. (1986) also reported that average BW at first egg was 3.9kg and 4.5kg for restricted and ad libitum-fed pullets, respectively, and peak production and cumulative egg numbers were higher for feedrestricted pullets. McDaniel and Brake (1981) used 5 feeding regimens (full feed and 4 rates of feed restriction) to feed Hubbard broiler breeders at 24 wk of age after a conventional skip a day restriction program. The authors found that breeders fed higher levels of feed exhibited lower egg production, poorer feed conversion, heavier BW and larger egg weights. The results were in agreement with the data reported in Table 2. The lower egg production of ad libitum-fed breeders in this study was probably due to their heavier BW similar to the findings by Robinson et al. (1993). The researchers found that overweight broiler breeders exhibit shorter laying sequences.

Table 8. Stepwise regression for predicting carcass protein and carcass fat with plasma hormone levels for feed-restricted breeders

Step	Variable entered ¹	\mathbb{R}^2	F-value	P > F
Carcass fat (%)	1 IGF-I	0.1632	19.5	< 0.0001
` ,	2 T ₄	0.215	6.53	0.0121
	3 Glucagon	0.2644	6.59	0.0118
	4 IGF-II	0.2841	2.67	0.1054
	5 Insulin	0.2932	1.23	0.2704
	6 Intogl	0.3084	2.09	0.1514
Carcass protein (%)	1 IGF-ĬI	0.3223	47.56	< 0.0001
1	2 T ₄	0.3829	9.71	0.0024
	3 Glucagon	0.4121	4.87	0.0297
	4 Insulin	0.4448	5.72	0.0187
	5 Leptin	0.4625	3.16	0.0786
	6 Intogl	0.4752	2.31	0.1322
	7 Estradiol	0.4875	2.24	0.1375
	8 T ₃	0.4978	1.91	0.1725
	9 IĞF-I	0.5010	0.60	0.4409

 $^{^{1}}$ IGF = insulin-like growth factor; T_4 = thyroxine; Intogl = M ratio of plasma insulin/glucagon; T_3 = triiodothyronine.

Research has not always shown that feed restriction programs improve the performance of breeders. Robbins et al. (1988) reported that broiler breeder females reared through 23 wk of age with a feed restriction program according to the breeder's recommendation and then provided feed ad libitum during lay produced more eggs than restricted pullets. Pym and Dillon (1974) also demonstrated that production of hatchable eggs per hen day to 67 wk of age was highest in pullets restricted during rearing and fed ad libitum during the laying period. Robinson and Sheridan (1982) reported that restricting feed intake of breeders by 7 to 8% during the laying period reduced hen-day and hen-housed egg numbers. Wilson et al. (1983) reported breeder pullets provided a feed restriction program during the egg production period consumed significantly less feed and weighed less than full fed breeder pullets. Egg production for breeders fed restricted amounts of feed was significantly lower than breeders fed ad libitum during colder months. However, the researchers observed that feed-restricted breeders laid at a higher rate during warmer months. In the authors' opinion, the variations in environmental ambient temperature, egg production rate, and genetic strains of breeders from previous research could easily account for the negative performance attributed to various amounts of feed restriction in the production unit.

Soller et al. (1984) observed that broiler breeder pullets entered lay at the same lean BW, percentage carcass ash, and percentage carcass protein content regardless of the degree of feed restriction during rearing. The pullets reached sexual maturity at a different age, carcass weight, carcass dry matter, and carcass fat content. Although the breeder pullets reported herein were only fed the 2 feeding programs from 21 wk of age, the data in Table 2 shows the breeder pullets fed ad libitum or feed restricted had similar amounts of total body protein (BW × % carcass protein) and different amounts of total carcass fat (BW × % carcass fat) at first egg indicating that body protein content is a major threshold for sexual maturity.

Plasma Hormones

There was a significant decline in IGF-I in the feed-restricted group at first egg compared with the feed-restricted pullets at the other periods. The ad libitum-fed breeders also had the lowest IGF-I level at first egg, but the level was not significantly lower than the IGF-I levels from the ad libitum-fed breeders at postlight stimulation and the 36.5 wk period. There are some indications of the role of IGF-I in the regulation of reproductive performance. IGF-I is expressed in the avian ovary (Roberts et al., 1994) and specific IGF-I receptors are present in the granulosa cells (Huybrechts et al., 1991). In vivo supplementation of IGF-I has been shown to change the in vitro LH sensitivity of the granulosa cells, which implicates a possible role of IGF-I in follicular maturation.

The IGF-I was higher in restricted pullets compared with those fed ad libitum (Table 4). The increased IGF-I in restricted pullets was in agreement with Hocking et al. (1994) who also found that the concentration of IGF-I was higher in restricted pullets compared with those fed ad libitum at 19 wk of age and there was no decline at the end of sampling period (30 wk). Bruggeman et al. (1997) reported feed-restricted pullets produced 2 equal peaks of plasma IGF-I concentration at 8 wk and 14 wk of age during the period from hatch to sexual maturity. Breeder pullets fed ad libitum only produced 1 peak at 10 wk of age during the same time period. Bruggeman et al. (1997) also reported that from 14 wk until 24 wk, IGF-I concentrations remained higher in the restricted group compared with the ad libitum fed group, but IGF-I concentrations were higher in the ad libitum-fed group compared with the restricted group from 2 to 14 wk. Bruggeman et al. (1997) also determined feed restriction produced higher plasma concentrations of GH and T₄ compared with hormone levels in the fully fed animals. The T₃ plasma concentrations were higher in the ad libitum-fed groups than in the restricted groups. In all groups, Bruggeman et al. (1997) found GH and T₃ concentrations decreased with advancing age, whereas T₄ increased during the same period. The research reported herein shows the T₃ levels were higher in ad libitum-fed breeders than in restricted breeders at the prelight stimulation period but there were no significant differences in T₃ at postlight stimulation, first egg, and 36.5 wk for breeders from either of the 2 feeding systems (Table 4). The T₄ level was 1.47 ng/mL higher in restricted pullets compared with ad libitum-fed breeder pullets at postlight stimulation period but there were no significant differences in T₄ levels at other physiological periods. Dewil et al. (1991) demonstrated that the granulosa cells of a fat broiler line showed a higher T₃ receptor number and a higher occupancy compared with a lean line with a better reproductive performance. The research by Dewil et al. (1991) supports the higher T₃ levels found in ad libitum-fed breeders with higher percentage carcass fat compared with the feed-restricted birds (Table 4). T₃ seems likely to have a role at the ovarian level. McMurtry et al. (1986) examined plasma GH, insulin, glucagon, T_3 , and T_4 and observed the insulin level was suppressed during and following restriction compared with ad libitum-fed controls, whereas glucagon was elevated. Feed restriction didn't alter the response to feeding for the other hormones. McMurtry et al. (1986) suggests the altered intogl relationship in the restricted chicks shows these hormones may be contributing to the reduced rate of lipid deposition and increased lean tissue accretion observed at 7 wk of age. Numerous studies have shown that changes occur in thyroid function when chicks are subjected to periods of fasting and refeeding (Harvey and Klandorf, 1983). During fasting, circulating T₃ is depressed while T₄ is increased. Similarly, insulin concentration was known to be suppressed following fasting (Rosebrough et al., 1984) and glucagon secretion is enhanced during fasting (Hazelwood, 1980). Dupont et al. (1999) demonstrated that a significant activation of early steps of insulin signaling in liver of ad libitum-fed chickens may at least partly account for their increased liver lipogenesis and ultimately their fattening.

There was no significant difference in the leptin level at the 36.5 wk period for the breeders fed by the 2 feeding systems. Leptin is secreted by adipose tissue and has been shown to play an important role in feed intake regulation, energy metabolism, and reproduction in mammals. Ashwell et al. (1999) reported that leptin expression in liver is increased by insulin and decreased by glucagon and estrogen in broiler chickens. The report by Ashwell et al. (1999) agrees with the data reported herein (Table 4) that leptin level was low in feed-restricted pullets when insulin level was low and glucagon level was high, but leptin level was high in ad libitm fed pullets when insulin level was high and glucagon level was low. Taouis et al. (2001) indicated that chicken leptin expression is regulated by hormonal and nutritional status. The researchers suggested the regulation of leptin expression was tissue-specific with a high sensitivity in the liver compared with adipose tissue. The blood leptin levels were regulated by the nutritional status with high levels appearing in the fed state compared with the fasted state. This was in agreement with the data from Table 4 showing the leptin concentration was higher in ad libitum-fed breeders than in feed-restricted breeders. Ashwell et al. (2001) reported that metabolic BW and adipose leptin expression were positively correlated. The research group suggested leptin may be involved in lipid flux through the adipocyte as well as the shift in lipid metabolism to increased storage during prepuberty. The results from Ashwell et al. (2001) also concurred with the data reported herein that ad libitum breeders were heavier than restricted breeders and the leptin concentration was higher in ad libitum-fed breeders than in feed-restricted breeders (Table 4). Renema et al. (1999b) found that the highest 17β estradiol concentration occurred 5.69d (feed-restricted pullets) and 6.63d (ad libitum-fed pullets) prior to sexual maturity and was very consistent within each feeding regimen. The finding was in agreement with the data reported herein that plasma 17β -estradiol concentration was at the highest at postphotostimulation and first egg for both feeding systems. Renema et al. (1999b) found that the highest plasma 17β -estradiol concentration of restricted pullets was greater than that of the ad libitumfed pullets. This finding was in disagreement with the data reported herein because the plasma 17β -estradiol concentration at peak production from feed-restricted breeders and breeders fed ad libitum were not significantly different (Table 4).

Stepwise regression indicated that T_4 was the most important hormone for predicting the carcass fat in ad libitum-fed pullets and T_3 was the most important hormone for predicting carcass protein (Table 6). The 2 thyroid hormones were each very similar on a correlation basis to the percentage carcass fat and percentage

carcass protein with each hormone being negatively correlated to the percentage carcass fat and positively correlated to the percentage carcass protein (Table 5). The interesting aspect of the thyroid hormone correlation to body composition of breeders was when the breeders were fed restricted amounts of feed. The T_3 hormone for the feed-restricted breeders did not correlate with either percentage carcass fat or percentage carcass protein (Table 7). The T_4 hormone remained consistent for correlating to body composition in the feed-restricted breeders and the hormone concentration produced a significant negative correlation ($R^2 = -0.3348$; P = 0.0003) to percentage carcass fat and a positive correlation ($R^2 = 0.4480$; P < 0.0001) to percentage carcass protein.

The IGF-I and IGF-II hormones showed a correlation to percentage carcass fat and percentage carcass protein for the ad libitum-fed breeders (Table 5) but the correlations were even higher for the feed-restricted breeders (Table 7). An interesting observation was the 2 hormones reacted in opposite directions for ad libitum-fed breeders with the IGF-I hormone concentration negatively correlating ($R^2 = -0.3243$; P = 0.0005) to percentage carcass fat and IGF-II positively correlating ($R^2 = 0.2882$; P = 0.0023) to carcass fat. The 2 hormones also responded in an opposite direction when associated with the percentage carcass protein for ad libitum-fed breeders. The IGF-I plasma concentration was positively correlated to percentage carcass protein ($R^2 = 0.4253$; P < 0.0001) and IGF-II was negatively correlated to percentage carcass protein ($R^2 = -0.1742$; P = 0.07). The IGF-I and IGF-II hormones were both negatively correlated to percentage carcass fat and both positively correlated to percentage carcass protein for feed-restricted breeders. The reason that IGF-II would be positively correlated to percentage carcass fat and negatively correlated to percentage carcass protein for the ad libitum-fed breeders and respond in a completely opposite direction for feed-restricted breeders is not understood.

The FCPDMBW for ad libitum-fed breeders was positively correlated to insulin, leptin, T_3 , and intogl hormone concentrations and negatively correlated to IGF-II levels (Table 5). The ability to predict the potential feed consumption of these breeders using a 2 hormone index was very low ($R^2 = 0.087$), however the index was close to being significant (P = 0.0567; Table 6). The low correlation coefficient of the index used for predicting feed intake would most likely inhibit the usefulness of this as a genetic tool for selecting breeding stock. The index of hormones was not used for predicting FCPDMBW for feed-restricted breeders because the small differences in FCPDMBW were only from the differences in BW because all breeders from the restricted group were fed the same daily intake of feed.

Ovary Weight and Follicles

The total LYF weight followed the same trend as the LYF number which showed that ad libitum-fed breeders had heavier total LYF weight than restricted breeders

at first egg, and ad libitum-fed breeders had numerical heavier total LYF weight than restricted breeders at the postlight stimulation and 36.5-wk period. The number of LYF and the total weight of LYF were higher at first egg than at the 36.5-wk period in ad libitum-fed breeders, and the number of LYF and the total weight of LYF were higher at the 36.5-wk period than at postlight stimulation for feed-restricted breeders. Yu et al. (1992) reported that average number of large ovary follicles in RF pullets (restricted 4 to 18 wk and fed ad libitum afterwards) and RR pullets (restricted 4 to 18 wk and also restricted afterwards) at sexual maturity were 10.7 and 7.8, respectively, and stepwise regression indicated that BW was the most important among 11 variables in determining the number of large follicles in the ovaries of breeders at sexual maturity. Robinson et al. (1998) reported the weight of the LYF at sexual maturity was heavier in fast feed (larger feed allocation than slow feed hens from 20 to 25 wk) than slow feed (5 g or less weekly increase in feed allocation from 20 to 25 wk) hens. The gradual feeding program of the slow feed treatment may be a potential means of limiting follicle recruitment and thereby potentially increasing settable egg production compared with feeding programs using more rapidly increasing feed allocations.

Renema et al. (1999b) reported that the ad libitum fed pullets reached sexual maturity with 11.0 LYF compared with 7.1 in feed-restricted pullets which was in agreement with the data reported herein (Table 3). The authors also reported that the extent of small follicle atresia in feed-restricted pullets was inversely proportional to LYF number by stepwise regression, and increased small follicle atresia was associated with a longer sexual maturation period in feed-restricted pullets at photostimulation which was in disagreement with the data reported herein.

Bruggeman et al. (1999) reported that the absolute weight of the ovary of different feeding groups didn't differ and the authors suggested that a threshold of ovary weight must be achieved before sexual maturity is attained. Their finding was in disagreement with the data reported herein in Table 3, which showed the pullets fed ad libitum had heavier ovary weight compared with the feed-restricted pullets at first egg and the 36.5wk period. The data in Table 3 also shows the number of small atretic ovarian follicles and stroma weight was also higher in ad libitum fed pullets compared with feed-restricted pullets. Hocking et al. (1989) have shown that increased rates of follicular maturation and atresia are characteristic of broiler breeders fed ad libitum during rearing and the author observed that restricting feed intake of broiler breeder hens beyond 15 wk of age reduced the number of large follicles. Robinson et al. (1991) conducted a study with hens that were feed restricted comparable with industry feed restriction programs until 34 wk of age and then provided the breeders a short-term exposure to ad libitum feeding. The weight of the ovarian stroma representing the pool of small nonhierarchical follicles was increased by 1.3 and 3.9 g after 7 or 14 d of ad libitum feeding, respectively, which was in agreement with the data reported herein (Table 3). Robinson et al. (1991) have suggested a heavier stroma may indicate greater numbers of 17β -estradiol producing follicles, thereby affecting total 17β -estradiol output of these ovaries. The data from Table 4 indicated the concentration of 17β -estradiol in ad libitum pullets was numerically higher than restricted feeding pullets at first egg period.

At photostimulation there was a difference in 17β -estradiol due to feeding system, with ad libitum fed pullets exhibiting higher plasma 17β -estradiol compared with the feed-restricted breeders. This result suggested that some initial maturation had occurred in the ovaries of ad libitum fed pullets prior to photostimulation. Ovary weights of ad libitum fed pullets indicated that they may be at a more advanced developmental level than in the feed-restricted pullets. Renema et al. (1999b) demonstrated that ovary weight correlated with BW (r = 0.512; P = 0.004) and with fat pad weight (r = 0.837; P = 0.003), and peak 17β -estradiol concentration correlated with the total weight of the LYF (r = 0.512; P = 0.005), which was in agreement with the data from Table 3.

In summary, the breeders fed ad libitum become obese after consuming too much feed, had too many LYF, produced larger numbers of abnormal eggs and fewer normal eggs after sexual maturity. The plasma hormones from these breeders fed ad libitum were significantly correlated with the body composition changes that occurred from prelight stimulation to 36.5 wk following peak egg production. One of the objectives was to determine if a metabolic hormone index could be used as a genetic tool for future breeder selection allowing primary breeders to regulate feed intake of progeny. The low correlation coefficient for predicting the FCPDMBW differences in the breeders shows the metabolic hormone index may not be an adequate method for predicting feed consumption. Breeders that were feed restricted produced significantly more normal eggs with less feed consumed as expected, had lower percentage carcass fat and higher percentage carcass protein. A metabolic hormone index may be useful for predicting the body composition of feed-restricted breeders similar to ad libitum fed breeders. The research shows that total carcass protein for both ad libitum fed and feed restricted breeders was similar at first egg indicating the importance of protein mass needed for sexual maturity. The BW and total carcass fat at first egg or sexual maturity were different for the 2 feeding systems. The possibility of using a stepwise regression index that includes IGF-II, T₄, insulin, and glucagon levels for predicting percentage carcass protein for feed-restricted pullets may be useful in helping make management decisions regarding physiological readiness for sexual maturity and photostimulation.

REFERENCES

AOAC. 1990. Official Methods of Analysis. 15th ed. Assoc. Off. Anal. Chem., Washington, DC.

- Ashwell, C. M., S. M. Czerwinski, D. M. Brocht, and J. P. McMurtry. 1999. Hormonal regulation of leptin expression in broiler chickens. Am. J. Physiol. 276:R226–R232.
- Ashwell, C. M., M. P. Richards, and J. P. McMurtry. 2001. The ontogeny of leptin mRNA expression in growing broilers and its relationship to metabolic BW. Domest. Anim. Endocrinol. 21:161–168.
- Bornstein, S., I. Plavnik, and Y. Lev. 1984. Body weight and/ or fatness as potential determinants of the onset of egg production in broiler breeder hens. Br. Poult. Sci. 25:323– 342
- Bruggeman, V., O. Onagbesan, E. D'Hondt, N. Buys, M. Safi, D. Vanmontfort, L. Berghman, F. Vandesande, and E. Decuypere. 1999. Effects of timing and duration of feed restriction during rearing on reproductive characteristics in broiler breeder females. Poult. Sci. 78:1424–1434.
- Bruggeman, V., D. Vanmontfort, R. Renaville, D. Portetelle, and E. Decuypere. 1997. The effect of feed intake from two weeks of age to sexual maturity on plasma growth hormone, insulin-like growth factor-I, insulin-like growth factor-binding proteins, and thyroid hormones in female broiler breeder chickens. Gen. Comp. Endocrinol. 107:212–220.
- Cobb-Vantress. 2002. Cobb 500 Breeder Management Guide. Blueprint for Success. Cobb-Vantress, Siloam Springs, AR.
- Decuypere, E., and E. Kuhn. 1984. Effect of fasting and feeding time on circadian rhythms of serum thyroid hormone concentrations, glucose, liver monodeiodinase activity and rectal temperature in growing chickens. Domest. Anim. Endocrinol. 1:251–262.
- Dewil, E., L. M. Huybretchts, E. Decuypere, F. R. Leenstra, and E. R. Kuhn. 1991. Evidence for a nuclear T₃-receptor in the ovarian tissue of lean and fat strain of chickens. Med. Sci. Res. 1:771–772.
- Dupont, J., J. Chen, M. Derouet, J. Simon, B. Leclerq, and M. Taouis. 1999. Metabolic differences between genetically lean and fat chickens are partly attributed to the alteration of insulin signaling in liver. J. Nutr. 129:1937–1944.
- Evock-Clover, Č. M., Š. Poch, M. Richards, C. Ashwell, and J. P. McMurtry. 2002. Expression of an uncoupling protein gene homolog in chickens. Comp. Biochem. Physiol. 133:345–358.
- Harvey, S., and H. Klandorf. 1983. Reduced adrenocortical function and increased thyroid function in fasted and refed chickens. J. Endocr. 98:129–135.
- Hazelwood, R. 1980. The avian gastro-enteric-pancreatic system: Structure and function. Pages 231–250 in Avian Endocrinology. A. Epple and M. Stetson, ed., Academic Press, New York, NY.
- Hillgartner, F. B., L. M. Salati, and A. G. Goodridge. 1995. Physiological and molecular mechanisms involved in nutritional regulation of fatty acid synthesis. Physiol. Rev. 75:47–76.
- Hocking, P. M. 1990. Comparison of the effects of the degree of food restriction during rearing on ovarian function at the onset of lay in unselected ducks and in a line selected for improved feed efficiency. Br. Poult. Sci. 31:351–359.
- Hocking, P. M. 1993. Effects of body weight at sexual maturity and the degree and age of restriction during rearing on the ovarian follicular hierarchy of broiler breeder females. Br. Poult. Sci. 34:777–784.
- Hocking, P. M., R. Bernard, and G. W. Robertson. 2002. Effects of low dietary protein and different allocations of feed during rearing and restricted feeding after peak rate of lay on egg production, fertility and hatchability in female broiler breeders. Br. Poult. Sci. 43:94–103.
- Hocking, P. M., R. Bernard, R. S. Wilkie, and G. Goddard. 1994. Plasma growth hormone and insulin-like growth factor-I (IGF-I) concentrations at the onset of lay in ad libitum and restricted broiler breeder fowl. Br. Poult. Sci. 35:299–308.

- Hocking, P. M., D. Waddington, M. A. Walker, and A. B. Gilbert. 1989. Control of the development of the ovarian follicular hierarchy in broiler breeder pullets by feed restriction during rearing. Br. Poult. Sci. 30:161–174.
- Huybrechts, L. M., E. Decuypere, and E. R. Kuhn. 1991. Granulosa cells of the preovulatory follicles of domestic fowl contain an insulin-like growth factor (IGF) receptor. Med. Sci. Res. 19:699–700.
- Joseph, N. S., F. E. Robinson, D. R. Korver, and R. A. Renema. 2000. Effect of dietary protein intake during the pullet-tobreeder transition period on early egg weight and production in broiler breeders. Poult. Sci. 79:1790–1796.
- Lauterio, T. J., and C. G. Scanes. 1987. Hormonal responses to protein restriction in two strains of chickens with different growth characteristics. J. Nutr. 117:758–763.
- Lilburn, M. S., and D. J. Myers-Miller. 1990. Effect of BW, feed allowance, and dietary protein intake during the prebreeder period on early reproductive performance of broiler breeder hens. Poult. Sci. 69:1118–1125.
- McDaniel, G. R., and J. Brake. 1981. Factors affecting broiler breeder performance. 1. Relationship of daily feed intake level to reproductive performance of pullets. Poult. Sci. 60:307–312.
- McGuinness, M. C., and L. A. Cogburn. 1990. Measurement of developmental changes in plasma insulin-like growth factor I levels of broiler chickens by radio-receptor assay and radioimmunoassay. Gen. Comp. Endocrinol. 79:446–458.
- McMurtry, J. P., G. L. Francis, F. Z. Upton, G. Rosselot, and D. M. Brocht. 1994. Developmental changes in chicken and turkey insulin-like growth factor-I (IGF-I) studied with a homologous radioimmunoassay for chicken IGF-I. J. Endocrinol. 142:225–234.
- McMurtry, J. P., I. Plavnik, R. W. Rosebrough, and J. A. Proudman. 1986. Metabolic hormone response to feeding in restricted broilers. Poult. Sci. 65(suppl. 1):92.
- McMurtry, J. P., I. Plavnik, R. W. Rosebrough, N. C. Steele, and J. A. Proudman. 1988. Effect of early feed restriction in male broiler chicks on plasma metabolic hormones during feed restriction and accelerated growth. Comp. Biochem. Physiol. 91A:67–70.
- McMurtry, J. P., R. W. Rosebrough, D. M. Brocht, G. L. Francis, Z. Upton, and P. Phelps. 1998. Assessment of developmental changes in chicken and turkey insulin-like growth factor-II (cIGF-II) by homologous radioimmunoassay. J. Endocrinol. 157:463–473.
- McMurtry, J. P., R. W. Rosebrough, and N. C. Steele. 1983. An homologous radioimmunoassay for chicken insulin. Poult. Sci. 62:697–701.
- Pym, R. A. E., and J. F. Dillon. 1974. Restricted feed intake and reproductive performance of broiler breeder pullets. Br. Poult. Sci. 15:245–259.
- Renaville, R., A. Devolder, S. Massart, M. Sneyers, A. Burny, and D. Portetelle. 1993. Changes in the hypophysial-gonadal axis during the onset of puberty in young bulls. J. Reprod. Fertil. 99:443–449.
- Renema, R. A., F. E. Robinson, J. A. Proudman, M. Newcombe, and R. I. McKay. 1999a. Effects of BW and feed allocation during sexual maturation in broiler breeder hens. 1. Growth and carcass characteristics. Poult. Sci. 78:629–639.
- Renema, R. A., F. E. Robinson, J. A. Proudman, M. Newcombe, and R. I. McKay. 1999b. Effects of BW and feed allocation during sexual maturation in broiler breeder hens. 2. Ovarian morphology and plasma hormone profiles. Poult. Sci. 78:619–628.
- Robbins, K. R., S. F. Chin, G. C. McGhee, and K. D. Roberson. 1988. Effects of ad libitum versus restricted feeding on body composition and egg production of broiler breeders. Poult. Sci. 67:1001–1007.
- Robbins, K. R., G. C. McGhee, P. Osei, and R. E. Beauchene. 1986. Effects of feed restriction on growth, body composi-

tion, and egg production of broiler females through 68 weeks of age. Poult. Sci. 65:2226–2231.

- Roberts, R. D., P. J. Sharp, D. W. Burt, and C. Goddard. 1994. Insulin-like growth factor-I in the ovary of the laying hen: Gene expression and biological actions on granulosa and thecal cells. Gen. Comp. Endocrinol. 93:327–336.
- Robinson, D., and A. K. Sheridan. 1982. Effects of restricted feeding in the growing and laying periods on the performance of white leghorn by Australorp crossbred and white leghorn strain cross chickens. Br. Poult. Sci. 23:199–214.
- Robinson, F. E., R. A. Renema, J. J. R. Feddes, J. L. Willson, M. Newcombe, and R. I. Mckay. 1998. Effects of photostimulatory lighting and feed allocation in female broiler breeders. 1. Reproductive development. Can. J. Anim. Sci. 78:603–613.
- Robinson, F. E., J. L. Willson, M. W. Yu, G. M. Fasenko, and R. T. Hardin. 1993. The relationship between body weight and reproductive efficiency in meat-type chicken. Poult. Sci. 72:912–922.
- Robinson, F. E., M. W. Yu, R. T. Hardin, M. E. Lupicki, and R. G. Charles. 1991. The short-term consequences of a sudden increase in feed allowance in broiler breeder hens. Poult. Sci. 70(Suppl. 1):100. (Abstr.)

- Rosebrough, R., J. McMurtry, M. Richards, and N. Steele. 1984. Effect of starvation-refeeding and an exogenous glucocorticoid on carbohydrate metabolism is chick liver. Poult. Sci. 63:2444–2449.
- Siegel, P. B., and E. A. Dunnington. 1985. Reproductive complications associated with selection for broiler growth. Pages 59–72 in Poultry Genetics and Breeding. W. G. Hill, J. M. Manson, and D. Hewitt, ed. Br. Poult. Sci. Ltd., Harlow, UK.
- Soller, M., Y. Eitan, and T. Brody. 1984. Effect of diet and early quantitative feed restriction on the minimum weight requirement for onset of sexual maturity in white rock broiler breeders. Poult. Sci. 63:1255–1261.
- Taouis, M., S. Dridi, S. Cassy, Y. N. Benomar, N. Rideau, M. Picard, J. Williams, and A. Gertler. 2001. Chicken leptin: Properties and actions. Domest. Anim. Endocrinol. 21:319–327.
- Wilson, H. R., D. R. Ingram, and R. H. Harms. 1983. Restricted feeding of broiler breeders. Poult. Sci. 62:1133–1141.
- Yu, M. W., F. E. Robinson, and A. R. Robblee. 1992. Effect of feed allowance during rearing and breeding on female broiler breeders. 1. Growth and carcass characteristics. Poult. Sci. 71:1739–1749.